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PROTISTAN PHYLOGENY AS INDICATED BY THE FOSSIL RECORD

*Alfred R. Loeblich, Jr.**

Summary

Even though the fossil record is incomplete and perhaps difficult to use in phylogenetic studies of the Protista, in the last resort it is the true basis for any real phylogeny as the dimension of time must be taken into consideration. Other hypothetical phylogenies represent speculation based on analysis of a single time plane. Major algal differentiation was a series of ancient events that took place early in the Precambrian and preceded the diversification of the animal kingdom. Every plant division, five of the classes and seven orders of plants, are represented by fossils of Precambrian age. In addition over 1500 described cyst species of some algal group (= Hystrichophyta or Acritarcha) occur in the Precambrian and Paleozoic, that may eventually fill in some of the gaps in the fossil record of the algae and contribute to a refinement of any future phylogenetic studies. With the increasing cooperation developing today between modern biologists and paleontologists interested in phylogenetic studies, I am optimistic for the future of this interesting and highly speculative field.

Introduction

Many writers have deplored the inadequacy of the fossil record for the formulation of reasonable phylogenies of both plants and animals, especially those concerning algae and protozoans. Lacking an adequate fossil record, biologists of both disciplines ignore the time dimension, and in constructing phylogenies they assume that different levels of organisation found in living taxa resemble the ancestral forms that were present in the geologic past. However, Bigelow (1958 :52) states, "The reconstruction of phylogeny using fossil evidence, is without doubt one of the most important and one of the most interesting activities of biology. Whether or not it can be accomplished accurately without fossil evidence, however, is very much open to question."

Certainly any proposed protistan phylogeny is speculative, perhaps especially those based entirely on fossils, for in addition to the inadequacies of the protistan fossil record, soft parts are lacking and hence little intracellular information can be obtained (e.g., of biochemical nature, nuclear character, flagellar structure, etc.). Nevertheless, many groups do have an abundant fossil record that can supplement living material in the construction of phylogenies. While biologists commonly are not aware of this abundant geological record, paleontologists commonly are not well versed on modern biological progress, even in their own field of specialization.

* Department of Geology, University of California, Los Angeles, California, 90024, U.S.A. and Chevron Oil Field Research Company, La Habra, California, 90631, U.S.A.

Problems presented by the geological record

As the geologic record supplied by sediments deposited in the past is incomplete, it cannot provide a complete and continuous record. Newell (1972 : 198) has postulated that non-sequence accounts for one-half to 99% of most rock sections. Even in the ocean basins, oceanic sequences of sediments are notoriously incomplete, and sediments of early Mesozoic age and older have been destroyed by crustal subduction. In areas where Precambrian sediments are exposed, much of the sequence is unfavorable for preservation of recognizable fossils. Fossils thus far obtained probably represent limited environments but widely dispersed areas, and are separated by immense amounts of time. In addition, freshwater deposits are uncommon in the geologic record, especially in the Precambrian and Early Paleozoic.

Preservation of recognizable fossils is a major problem for the protistan geologic record. Biologically deposited silica is in the unstable hydrated opaline form and siliceous microfossils other than the Radiolaria are generally absent from the Paleozoic rocks. Even the radiolarian skeletons have been recrystallized. The dispersed silica and amorphous cherts in Paleozoic and younger rocks may represent former siliceous skeletal remains whose source material is no longer recognizable.

Skeletal calcium carbonate is formed either as calcite or aragonite. In the plant kingdom the more stable calcite occurs in the blue-green and some red algae, coccolithophorids, discoasters, Dinophyceae and charophytes; and in the animal kingdom occurs in the foraminifers and tintinnids. Aragonite characterizes the foraminiferal superfamily Robertinacea, the green and some red and brown algae (Tappan and Loeblich 1971 : 253). Aragonite is less stable and may be removed by solution even where calcite is perfectly preserved.

Cellulose is readily hydrolyzed by bacterial action and rarely preserved as such in the rock record but certain other organic compounds may be exceptionally well preserved. The hydrocarbons phytane and pristane, which may be produced by alteration of chlorophyll have been identified in rocks as old as 3 b. y. The spore-pollen wall of higher plants, and the cyst wall of prasinophycean and other algae are composed of sporopollenins, a class of biopolymers derived by oxidative polymerisation of carotenoids and/or carotenoid esters (Brooks and Shaw 1972 : 69). The material of which the hystrichophyte (acritarch) and dinoflagellate cysts are constructed also has chemical properties similar to sporopollenin. Sporopollenin and these related compounds chemically are very stable, and are of common occurrence in algal cysts from the Early Proterozoic to the present, spanning about 2.5 b. y. Oxidation (weathering) of enclosing rocks or sediments will destroy such compounds and their preservation also is affected by the amount of heat or pressure to which the enclosing rocks were subjected. Organic microfossils may withstand rock temperatures up to about 300° C and remain recognizable (Jekhowsky 1958 : 1406).

Various algal cysts with a calcareous, siliceous or organic wall are abundant and well preserved throughout the geological column since the Late Precambrian, but many of these are difficult or impossible to assign to a precise algal group. Phycologists commonly report that an organism may develop thick-walled cysts, but they rarely figure the cyst morphology or mention its composition, although such a figure and a statement as to

composition would be of immense value to a paleontologist. Lacking precise compositional data, an indication would be useful as to whether or not the cyst would dissolve in one or another of the acids HCl. HF, or HNO_3. Such information for living taxa would make it possible to identify fossil representatives and thus extend back in time the range of many groups.

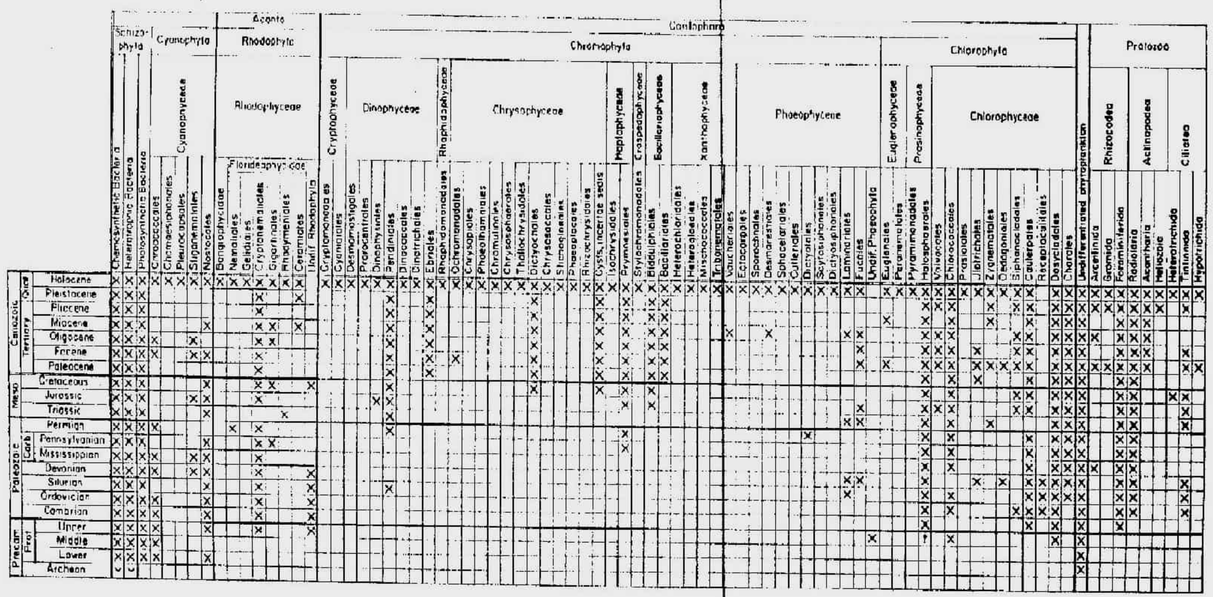
A notable exception to this dearth of information applicable to the micropaleontologists' use was an excellent and very useful contribution by Boalch and Parke (1971 : 99). Cysts of many modern *Pachysphaera* and *Pterosperma* were figured, and their composition was indicated as allied to sporopollenin. On the basis of this single contribution a large number of Paleozoic and Mesozoic genera now can be assigned unquestionably to an extant family, order and class. The antiquity of this group, already suggested by Manton and Parke (1965 : 753) from a study of modern forms, now is substantiated beautifully by the fossil record.

Knowledge of the composition of other modern cysts would immeasurably aid the paleontologist in determining the true affinities of the fossil cysts known as Acritarcha (Evitt 1963 : 300). The term acritarch which indicates an uncertain or confused origin was proposed as an informal "group", without nomenclatural status. Acritarchs were said to represent a variety of life stages (e.g., eggs, cysts, mature tests) of one-celled and multicellular plants and animals. Some have been demonstrated to be green algae or dinoflagellates, and some others probably are dinoflagellates that lack the minimum of morphological features required for recognition; most certainly the majority represent the cysts of phytoplankton organisms, and probably none of the acritarchs are derived from animals. Evitt's Group Acritarcha later was subdivided on gross morphology into 13 "subgroups" (Downie, Evitt and Sarjeant 1963 : 6). This highly artificial classification results in fossil genera which could be assigned to a single extant algal family being placed in separate morphologically unrelated subgroups. As originally defined, the subgroups also included pollen and dinoflagellates in addition to true "acritarchs".

Mädler (1963 : 317) proposed the Class Hystrichophyta, for fossil algae *incertae sedis*, including some acritarchs, dinoflagellates and other genera which are undoubted members of the modern class Prasinophyceae. Although Mädler's new class as originally conceived has little validity, for it includes genera belonging to two extant valid classes as well as some genera referrable to Evitt's Acritarcha, it included only the algae and excluded the animals.

Downie (1973 : 248) proposed a tentative subdivision of the "acritarchs" into ten related groups, as follows: *Pachysphaera, Tasmanites, Pterospermopsis, Baltisphaeridium, Navifusa,* Sphaeromorph acritarchs, *Micrhystridium-Veryhachium, Leiofusa, Acanthodiacrodium* and *Visbysphaera.* According to Downie, these groups include over ninety percent of the described acritarch species and genera, the remainder being left as "other acritarchs". The first five of these groups had features relating them to the Class Prasinophyceae; the Sphaeromorph acritarchs were considered as primitive and polyphyletic and probably include the ancestors of other algal groups represented among the acritarchs. The last four groups show possible affinities with the dinoflagellates, although the evidence for this was admittedly superficial and inconclusive. Like the earlier groupings proposed by Downie, Evitt and Sarjeant (1963 : 6) these groups include morphological types that clearly are unrelated (see Downie 1973 : 255 for

Fig. 1. Geologic ranges, as presently known, to the level of the Order for major groups of Protista and Monera (bacteria and blue-green algae).



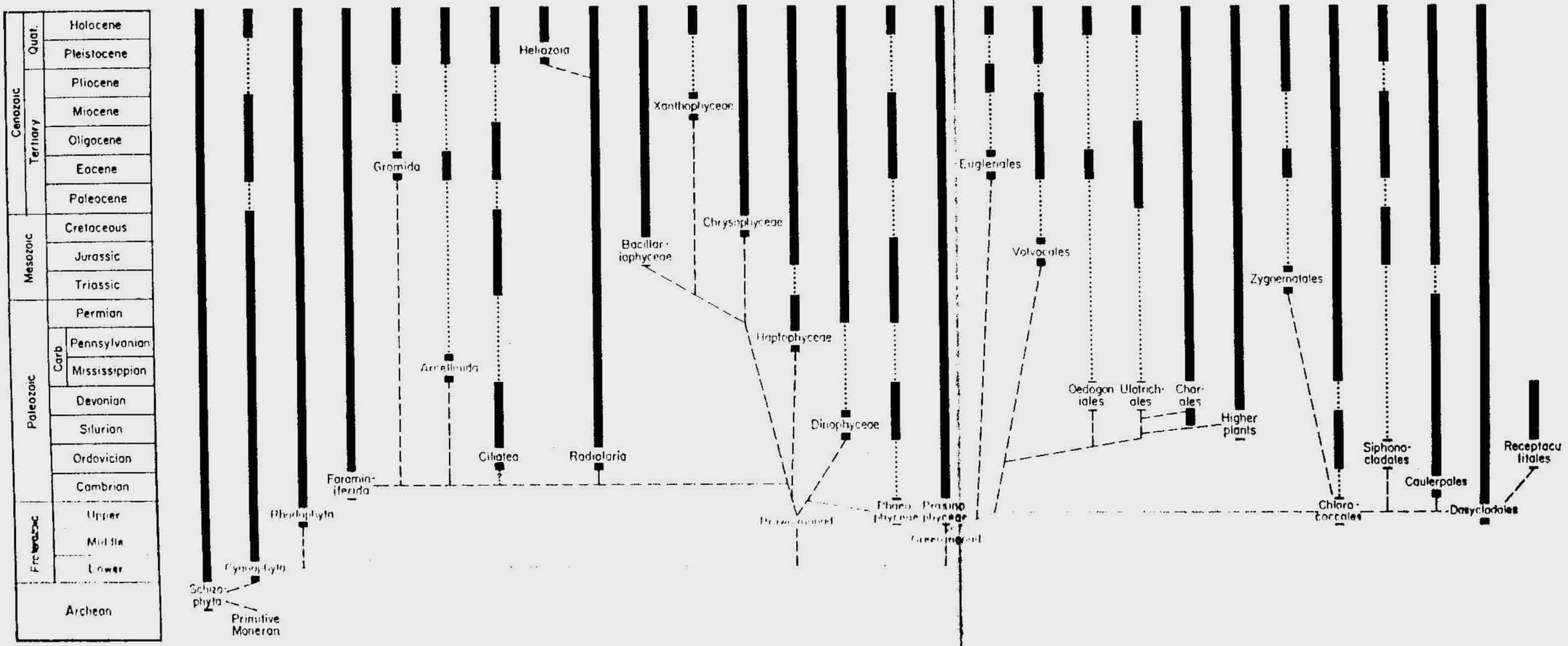
genera placed in the various groups). Thus, rather than follow the use of artificial groupings, I propose that both the terms Acritarcha and Hystrichophyta be abandoned, together with the use of subgroups or any arrangement of morphologic groupings or those based on inferences unsubstantiated by factual evidence. Some genera will be removed from the artificial categories and assigned their true systematic position, and the remainder should probably be discussed and arranged in alphabetical order as "undifferentiated phytoplankton" or "phytoplankton incertae sedis" until evidence is sufficient to assign their correct systematic position. The proliferation of terms or categories in a highly artificial scheme of classification serves no useful purpose, and insofar as it implies a definite taxonomic assignment may in fact deter true progress.

Probably the most important point in consideration of the fossil record for phylogenetic studies is the paucity of usable characters of unquestioned meaning. Intracellular structures such as nuclei, chloroplasts, pyrenoids, etc. have not been identified without doubt. The reports of nuclei in organisms from the Precambrian are questioned by Awramik, Golubić and Barghoorn (1972 : 438) and suggested to represent the cytoplasm of the entire cell which had been shrunken into a coagulated mass (pseudonucleus) within the globular envelope. Even the tapering of terminal cells described in filamentous blue-green algal fossils was shown to be like that produced by post-mortem shrinkage. Pigment and storage product character cannot be determined, nor can changes be detected in the biochemistry of the extinct organisms. No flagella, cilia or other such structures have been preserved in the fossil record. In fact, gross cell morphology and skeletal structure are the only characters preserved for consideration. Even these may be suspect, for similar morphologies occur in widely divergent groups of algae, and morphologic similarities between fossils and living organisms may or may not signify relationships. The only preservable fossil remains of the organic and certain siliceous and calcareous-walled phytoplankton are their cysts, which may bear little resemblance to the vegetative stage. Even the first known occurrence of an organism in geologic time may change as new data accumulate. Major new groups of organisms appear suddenly in the geologic record, seemingly fully developed and with little indication as to the identity of their ancestors. The period of time involved in their development may be unrepresented by sediments, the early forms may have been incapable of fossilization, or else we just cannot recognize and relate them. Yet with all these drawbacks inherent in the fossil record, the excellent record back in time for a number of major groups is useful and instructive for the determination of phylogenies.

Geologic range and phylogeny of some major groups of protistans

I have attempted to show (fig. 1) the geological ranges as presently known to the level of the Order for major groups of Protista and a portion of the Monera (bacteria and blue-green algae), if one uses the latter in the sense of Dougherty (1955 : 148). The classification used herein for the algae is that of Christensen (1966), except that the Loxophyceae has been combined with the Prasinophyceae (following Parke, in Parke and Dixon 1968 : 815); furthermore, I have added to the Chlorophyceae the fossil Order Receptaculitales, which is closely related to the Dasycladales (Rietschel 1969 : 465); the Order Ebriales is added to the Dinophyceae. The undifferentiated phytoplankton, in a column after the Chlorophyta in-

Fig. 2. Proposed phylogeny for all Classes and Orders of the Protista and Monera having a fossil record. Known fossil occurrence is shown in heavy black lines, gaps in occurrence by dotted lines, and hypothetical derivation with dashed lines.



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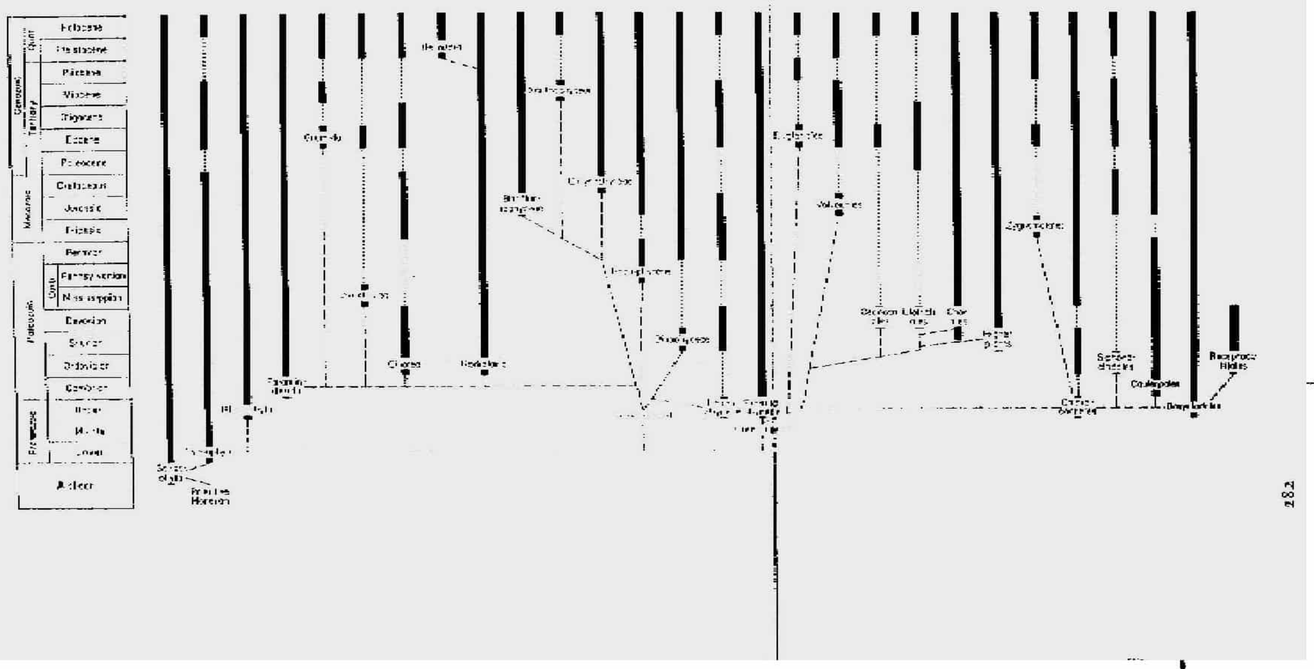

cludes a large group of diverse cysts, certainly of algal origin but of unknown exact affinity. A proposed phylogeny is developed for all classes and orders having a known fossil record (fig. 2).

The primitive moneran was probably heterotrophic and derived its energy from abiotically formed organic compounds, and gave rise to the chemosynthetic, heterotrophic and photosynthetic bacteria, the latter possessing bacteriochlorophyll and chlorobium chlorophyll. In the Early Proterozoic the Cyanophyta most probably arose from these photosynthetic bacteria by a series of mutations producing chlorophyll *a* and the phycobilins (phycocyanins and phycoerythrins). The development of chlorophyll *a* was one of the major events in the evolution of the algae and for the earth itself, for it allowed production of oxygen as a by-product of photosynthesis, and resulted in a profound change in the earth's atmosphere.

The Rhodophyta, possibly the most ancient eucaryotic group, arose in the Late Proterozoic. Of the two classes, the Bangiophycidae have no known fossil record, but the Florideophycidae have an uninterrupted one from Late Proterozoic to Holocene. Christensen (1966 : fig. 1) places both the Cyanophyta and Rhodophyta as branches off the main line of algal evolution. The Rhodophyta probably diverged shortly after the development of a membrane-bound nucleus. Klein and Cronquist (1967 : 227) favor the hypothesis that red algae and the other eucaryotes are not closely related and that the vesicular nucleus and membrane-bounded chloroplasts evolved independently in the red algae and in the green algae, but evidence for either pathway is at yet inconclusive. The Rhodophyta, here shown as an offshoot from the Cyanophyta – brown algal – green algal line probably are distant relatives of the blue-green by way of the Bangiophycidae (Papenfuss 1955 : 187). Both contain chlorophyll *a* as their primary photosynthetic pigment; both contain phycobilins, of which phycocyanins are dominant in the blue-greens and phycoerythrins in the red algae; chemically allied starch is the storage product in both, and both lack any flagellate stage. However, both Fott (1965 : 125) and Fritsch (1945b : 416) state that the Rhodophyceae show no clear relationship to any other class of algae. Although the Rhodophyta reach a high degree of complexity in the marine environment, they evidently represent an evolutionary dead-end that led to no other diversification.

Nearly contemporaneously with the appearance of the Rhodophyta in the Late Precambrian, two more branches, the Chromophyta and the Chlorophyta, diverged from the main algal line. The Chromophyta are characterized by chlorophyll *a* with certain classes having chlorophyll *c* as a subsidiary pigment and all members of the division lacking chlorophyll *b*. The Chlorophyta contain chlorophyll *b* in addition to chlorophyll *a*. Of prime consideration is that immediate ancestors of both of these divisions had developed the 9+2 structured flagellum, which is unknown in any previous group. The Chromophyta basically are heterokont and the Chlorophyta isokont in flagellation, but it must be noted that certain members of the chromophyte Class Haptophyceae are isokont and that the chlorophyte Classes Euglenophyceae and Prasinophyceae are heterokont. Manton (1965 : 7) commented that Christensen (1962 : fig. 1) placed Chromophyta and Chlorophyta at the same level, avoiding the question of which division had greater antiquity. A case could be made for a greater antiquity of certain Chromophyta that have chlorophyll *a* but no other chlorophyll (e. g., Xanthophyceae and Chrysophyceae), but the fossil record is inconclusi-

ve as the Phaeophyceae (which contain chlorophyll *c* in addition to chlorophyll *a*) and the Prasinophyceae (with chlorophyll *b*) appeared at about the same time in the Late Precambrian. Over 100 species of the undifferentiated phytoplankton have been described from the Precambrian, some of which possibly represent cysts of the Chromophyta (Tappan and Loeblich 1973), although their affinity at present is unproven. I suggest derivation of the Chromophyta from a brown, probably heterokont monad, the main evolutionary line being represented by the Chrysophyceae, although their earliest recognizable fossils are from the Lower Cretaceous (Dictyochales). In the Late Precambrian a line diverged leading to the Dinophyceae whose oldest unquestioned fossil is of Silurian age (Calandra 1964 : 4112). The line for the Dinophyceae represents the class as a whole, but the range as shown is that of the Order Peridiniales, which geologically appears to represent the ancestral Dinophyceae. During the Jurassic, the Dinophysiales diverged from this peridinialid line (*Nannoceratopsis* Deflandre 1948 : 183). The Dinophysiales are not represented (or not recognized) in post-Jurassic sediments until the Holocene. In the Paleocene a second branch from the peridinialid line represents the Ebriales, characterized by the absence of photosynthetic pigments, heterotrophic nutrition, heterokont flagella, a dinokaryon nucleus, and an internal siliceous skeleton of solid bars (Loeblich III *et al.* 1968). The Ebriales have an uninterrupted geologic record from Paleocene to Holocene. The Dinococcales are possibly represented in the Upper Cretaceous by *Palaeotetradinium* (Deflandre 1936 : 189), but the remaining orders of the Dinophyceae as yet have not been recognized as fossils.

From the dinophycean line the Phaeophyceae diverged very early in the Late Precambrian. Two fossil genera occur in the Late Precambrian Vendian of the U.S.S.R. (Gnilovskaya 1971 : 105) and 5 of the 10 orders have occurrences in the Silurian, Devonian, Permian, Triassic, Jurassic, Eocene, Oligocene and Miocene. The Phaeophyceae are a successful marine group but evidently form another evolutionary dead-end.

The only recognizable fossil Haptophyceae represent one family, the Coccolithophoraceae of the Order Prymnesiales. The Haptophyceae probably diverged from the main chrysophycean line early in the Paleozoic; the first recognizable fossil is from the Pennsylvanian of the United States (Gartner and Gentile 1973:401). Previous records from the Pennsylvanian of the United States (Noël 1961:3625) are thought to be due to contamination from later sediments and those mentioned by Noël from the Devonian, Mississippian and Permian were never described or figured. The Paleozoic forms figured and described by Deflandre (1970:2916) from the Siluro-Devonian and Mississippian have little in common with coccoliths of the Coccolithophoraceae except their range in size and probably are an entirely different group of organisms. The Paleozoic coccoliths mentioned by Gümbel (1870:766) were never described or figured and thus offer no solid evidence for a greater antiquity for the group. Coccolithophorids have been described from the Permian by Pirini Radrizzani (1971:993), are absent from the Triassic, but have a continuous record from the Early Jurassic to Holocene.

Of 11 modern orders of the Chrysophyceae, only two have a fossil record. The Order Dictyochales arose in the Early Cretaceous and has an excellent fossil representation from that time to the Holocene (see Loeblich III *et al.* 1968) and the *Ochromonadales* has an isolated record in the Eocene. However, there is an abundant recent and fossil record of siliceous cysts, both marine and freshwater, represented by the "artificial" families Archaeomonadaceae (marine taxa) and Chrysostomataceae (freshwater taxa). Similar cysts also occur in modern marine and freshwater sediments. Families, genera, and species based on these cysts are convenient for use by the paleontologist, but these are not comparable to modern taxa; the two "families" may include cysts of species of any of the 11 orders of extant Chrysophyceae. If cysts were described in detail for all members of the Chrysophyceae they might provide very important evidence for tracing lineages back in time.

The Bacillariophyceae probably diverged from the chrysophycean line before the Jurassic, for the earliest fossils are species of the centric diatom order Biddulphiales in the ε-Liassic Epoch of the Jurassic (Rothpletz 1896:910). These diatoms underwent an explosive development in the Cretaceous and early Tertiary, continuing to the present. In the Paleocene, the Bacillariales (pennate diatoms) originated from some unrecognized member or members of the Biddulphiales. Today, the pennates are perhaps the dominant group, occupying every conceivable environment while the centrics seem to be on the wane. The Bacillariophyceae may possibly have arisen earlier than the Jurassic; perhaps their ancestors were naked or weakly silicified and consequently not preserved, but no evidence is at hand to support such an hypothesis.

The Xanthophyceae diverged from the Bacillariophyceae line, but as they are poorly represented in the fossil record, the time of their appearance is unknown. A single representative of the Order Vaucheriales is known in the Miocene. Some Xanthophyceae produce silicified, endogenous bivalved cysts reminiscent of the earliest diatoms, that theoretically should be preserved in the geologic record. A number of the vegetative stages and aplanospores of the Xanthophyceae strikingly resemble certain Paleozoic cysts of undifferentiated phytoplankton. When the xanthophyte cysts are more completely described and their composition noted, many fossil cysts may prove to be related to this class.

Most of the protozoans (e.g. Foraminiferida, Arcellinida, Ciliatea, and Radiolaria) have an earlier and better fossil record than do their postulated ancestors. However, the protozoans are generally assumed to have originated from flagellated algal stocks. The earliest protozoans without mineralized skeletons could not be preserved, hence the early protozoan record is poor. Perhaps their ancestry lay within a chrysophyte lineage that might be represented in the undifferentiated phytoplankton although evidence is insufficient for assignment to their true systematic position.

Few electron microscopical studies have been made of the foraminifera other than their skeletons, but one significant study by Hedley, Parry and Wakefield (1968 : 149) determined that the gametes of the foraminifer *Boderia turneri* Wright have two heterokont flagella, the larger having a double row of hairs. Such a character is consistent with the hypothesis that the Foraminiferida were derived from the Chrysophyceae. The Order Rhizochrysidales of the Chrysophyceae contains a number of genera that develop a rhizopodial and amoeboid habit, lose their chromatophores and take up a holozoic nutrition. Probably the Foraminiferida that first appeared in the Cambrian arose from ancestors similar to these modern Rhizochrysidales; the Gromida first appeared in the Mississippian; and the Arcellinida has its oldest record in the Eocene.

The Radiolaria have been suggested to have originated from the silicoflagellates (Dictyochales of the Chrysophyceae) or from the Dinophyceae, but neither hypothesis appears likely. Probably the Radiolaria, Acantharia and Heliozoia arose from a chrysophyte ancestor, such as those forms in the Chromulinales that develop axopodia, and lose both their flagella and chromatophores. The Radiolaria have an uninterrupted fossil range from Ordovician to Holocene; the Acantharia from Eocene to Holocene; and the Heliozoia, Pleistocene to Holocene.

The Ciliatea are represented as fossils largely by the Order Tintinnida; fossils occur in the Ordovician through Devonian, Triassic through Cretaceous, Eocene and Oligocene, and Pleistocene-Holocene. The Order Heterotrichida is represented by a single Cretaceous occurrence and the Hypotrichida similarly by a single Eocene record. The Ciliatea are an exceedingly highly developed group of Protozoa with unknown ancestors. They are questionably derived here from the chrysophycean line, but no real evidence supports this assumption.

The Chlorophyta represent the final main divergence of the algae in the Precambrian. They are here indicated as originating from a hypothetical primitive green monad containing both chlorophyll *b* and chlorophyll *a*. Commonly the Order Volvocales of the Chlorophyceae is placed at the base in algal phylogenies, and other lineages are derived from that stock. However, this order first appears in the Jurassic. From the fossil record and the work of Manton and Parke (1965:743), I have placed the Prasinophyceae at the base of the Chlorophyta lineage. The Late Precambrian genus *Pterospermopsimorpha* is very probably a member of the Order Halosphaerales (Prasinophyceae); a number of other cysts, from the Cambrian to Holocene, with little doubt can be assigned to the same order (e.g., Family Pterospermataceae: *Tasmanites, Tytthodiscus, Pleurozonaria, Crassosphaera, Noremia, Discoidella, Duvernaysphaera, Pterosphaeridia, Pterospermella* (= in part *Pterospermopsis*), *Cymatiosphaera, Dictyotidium, Melikeriopalla*, and a number of genera as yet undescribed). Manton and Parke (1965:753) stated that the presence of scales and the absence of cellulose in the "theca" of the genus *Platymonas* (Prasinophyceae) are primitive characters, in themselves older than either chlorophyll *b* or a cell wall. The quadriflagellate *Platymonas* appears to be highly developed, but of course the primitive flagella and primitive flagellate have never been seen and we know nothing of the nature of either.

Klein and Cronquist (1967:233) comment that few phycologists will hypothesize as to the origin of the Euglenophyceae, but suggested that it might lie among the "Prasinovolvocales" of Chadefaud (1960:391). Euglenoids are here placed near the green algae and higher plants because of their mutual possession of chlorophylls *a* and *b*. But in most other features they appear closer to the Chromophyta than to the Chlorophyta: e.g., the carbohydrate storage product, paramylon, stored in the cytoplasm, is a β 1 : 3-linked glucan, as are laminarin of the Phaeophyceae and leucosin (chrysolaminarin) of the Chrysophyceae and Bacillariophyceae; the muciferous bodies, trichocysts, flagellar grooves and nuclear division are similar to those of some of the Dinophyceae; the flagella bear rows of long hairs as found in the Chrysophyceae, Xanthophyceae and Phaeophyceae; and neither periplast nor extracellular envelope contains cellulose, an important constituent of the Chlorophyceae and of the higher plants (Leedale 1967:3). The Euglenales has its first fossil record in the Eocene; it is evidently not closely related to any modern group, and must have had a long history, probably arising from an ancestral green monad in the late Precambrian.

The Volvocales and the Chlorococcales diverged from the green monad-Prasinophyceae line. The Chlorococcales have a good fossil record from the Late Precambrian to the Holocene with gaps in their geologic occurrence only in the Cambrian and Devonian. The Zygnematales have a fossil record in the Triassic, Eocene, and Pliocene to Holocene and are an offshoot from the Chlorococcales. The Chlorococcales also gave rise to the Siphonocladales whose first fossil record is Ordovician; the Caulerpales, first record in the Cambrian; the Dasycladales, with an uninterrupted record from Late Precambrian to Recent; and the fossil order Receptaculitales which ranges from Ordovician through the Devonian, with reports of scattered occurrences in the Carboniferous and Permian. The Receptaculitales are closely related to the Dasycladales. The ancestor to the siphonous groups probably was similar to such modern genera as *Protosiphon* or *Characiosiphon* (Fott 1965:122).

The Volvocales line (first fossils recognized in the Jurassic) apparently gave rise to the Oedogoniales and the Ulotrichales, although their first recognizable fossils are from the Devonian. The filamentous condition probably developed from a palmellate ancestor tending toward a filamentous direction such as occurs in *Palmodictyon*; if cell division should always occur in the same plane and if division stopped at two, rather than four or eight daughter cells, a simple filament would develop (Iyengar 1951:27), or repetitive simple vegetative division may have occurred along the same plane transverse to the long axis of the filament as Fritsch (1945a : 18) has outlined. From the Ulotrichales arose the Charales, whose oldest fossils are recorded from the uppermost Silurian. According to Desikachary and Sundaralingam (1962:13) a genus such as *Draparnaldiopsis* (Family Chaetophoraceae) suggests a close relationship to the Charales. Finally from the Ulotrichales and most probably from the Family Chaetophoraceae the higher land plants arose, possibly as early as Late Ordovician but certainly by the Early Silurian, for there is a good record of land plant spores in the Silurian.

The origin of the higher plants has been the subject of recent discussion and controversy. McBride (1970:366) believes that the ulotrichalean algae gave rise to the lower land plants, and that *Fritschiella* incorporates many of the characters that would be expected in the ancestor of the land plants. McBride (1970:370) believes *Fritschiella tuberosa* forms a crosswall by means of a centrifugal cell plate rather than by a centripetal furrowing of the cell wall material. However, neither the preprophase microtubules nor the phragmoplast microtubules were observed in *F. tuberosa*. According to Pickett-Heaps (1972:72), the hypothesis of the Ulotrichales being the progenitors of the land plants is partly based on the oversimplified recognition of only two types of cytokinesis – one in the algae (furrowing) and one in higher plants (cell plate formation). That is, if the latter is defined as the creation of a crosswall from fusing vesicles, diverse green algae also form cell plates. The existance of cell plates in Ulotrichalean algae does not take into account the distribution of microtubules around the cell plates. Pickett-Heaps discounts McBride's view that microtubules play no part in cell plate formation in *Fritschiella*. Microtubules are present in *Stigeoclonium* and, while their disposition and that of the daughter nuclei correspond

closely with that of many algae using phycoplast microtubules, they in no way correspond to the distribution of microtubules or daughter nuclei in the phragmoplasts of higher plants. Thus, according to Pickett-Heaps, if primitive Ulotrichalean algae did give rise to early land plants, one must explain how, when and why their cytokinesis changed from using phycoplast microtubular systems to phragmoplasts. He suggests (Pickett-Heaps 1972 : 74) that *Spirogyra* may be ancestral to higher plants, and that the primitive form of cytokinesis is perhaps even now evolving into the more advanced one utilizing a phragmoplast cell plate; *Chara* shows the closest analog to phragmoplasts of any of the algae, hence the Charophyceae could possibly have given rise to the higher plants, or at least be related to such progenitors of the far distant past.

Stewart, Mattox and Floyd (1973:135) concede the merit of Pickett-Heaps' view, but do not exclude the possibility that algae with phycoplasts gave rise to others with phragmoplasts.

This recent discussion of cytokinesis and its importance in phylogenetic reconstruction emphasizes the difficulty inherent in basing interpretations of ancestry solely on features of living plants, and the difficulty of determining which features were possessed by a Silurian or earlier ancestor to the land plants. Over the period of time from the appearance of the land plants in the Silurian to the present, more than one algal lineage may well have evolved from the phycoplast to the phragmoplast type; certainly living algae that appear transitional were not the ancestral forms in the Silurian some 400 million years ago. In a shorter period of time, vertebrate evolution has proceeded from the amphibians of the Devonian to man.

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